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# BOTANICAL GAZETTE

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OCTOBER 1896

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## THE PHALLOIDEÆ OF THE UNITED STATES.

### I. DEVELOPMENT OF THE RECEPTACULUM OF CLATHRUS COLUMNATUS Bosc.

EDWARD A. BURT.

(WITH PLATES XI AND XII)

In working out in *Anthurus borealis* the structural details of its imperfectly known genus, quite unexpected results were obtained with regard to the development of the receptaculum, which made it desirable to include in the investigation other representative genera of the Phalloideæ. A suitable range of additional forms was presented by *Mutinus caninus* (Huds.), *Dictyophora duplicata* (Bosc), and *Clathrus columnatus* Bosc, the two former of these belonging to the subfamily Phalleæ, and the *Clathrus* and the *Anthurus* to the Clathreæ. The papers on *Anthurus*<sup>1</sup> and *Mutinus*<sup>2</sup> have been published already. With the present paper on *Clathrus* it becomes possible to present more clearly the important developmental differences between the two subfamilies.

During the winter of 1894-5, a supply of alcoholic material of *Clathrus columnatus*, provided by Dr. Farlow, was studied

<sup>1</sup> A North American *Anthurus*, its structure and development. *Memoirs Boston Soc. of Nat. Hist.* 3:487. 1894.

<sup>2</sup> The development of *Mutinus caninus* (Huds.) Fr. *Annals of Botany* 10:343 1896.

under his direction in the Cryptogamic Laboratory of Harvard University. While fully substantiating the conclusion reached in the case of *Anthurus borealis* with regard to the origin of the chamber- and pseudoparenchymatous tissues of the receptaculum from different systems of primary tissues, nevertheless the range of stages was not great enough for a complete account of the development of the receptaculum. During the summer of 1895, a more abundant supply of young stages of *C. columnatus* was collected for me through the kindness of Professor P. H. Rolfs, of the Agricultural College, Lake City, Fla. With this the investigation has since been completed.

The methods of staining, etc., are given in detail in my former papers.

#### MATURE STAGE, INTRODUCING THE TERMS TO BE EMPLOYED.

The fructification of *Clathrus columnatus* has a receptaculum consisting of from two to five vertically ascending columns, which are quite separate where they arise from the volva, but join together at their apices. Usually there are only four such columns. These are joined together in pairs, the two opposite pairs being then connected together by a short and broad arch of the same nature as the columns. In the earlier stages the receptaculum is compressed into a small space in the interior of the fructification and enclosed by a fleshy bag called the volva. In such early stages the fructifications of this, and other members of the Phalloideæ, are called "eggs" on account of their general appearance.

By the time the spores mature, the egg attains a diameter of from 3 to 5<sup>cm</sup>. The receptaculum then elongates and bursts out through the apex of the volva, thus raising the spores to a height of from 5 to 8<sup>cm</sup> above the surface of the ground for more favorable dispersal. After elongation of the receptaculum, the spore-mass, or gleba, as it is called, may be seen as a spherical mass in the upper part of the main central cavity of the receptaculum, hanging from the under side of the arch and the proximate portions of the columns.

Of the three layers of the volva, the middle, or gelatinous layer, is not one continuous sheet as in the Phalleæ, but consists of as many meridionally arranged masses as the receptaculum has columns. These gelatinous masses alternate in position with the columns and are completely separated from each other by the cortical plates (*C'*, *figs. 4, 5, and 6*). The cortical plates extend from the base to the apex of the egg and connect each column of the receptaculum throughout its entire length with the outermost, or cortical layer (*C*). The peculiar arrangement of alternating cortical plates and gelatinous masses arises in the early differentiation of the egg, as will be shown further on.

#### COURSE OF DEVELOPMENT.

The eggs are borne at the ends of short branches of the subterranean mycelial strands. In cases where the egg has arisen as an outgrowth on the side of a mycelial strand, the portion of the strand beyond the egg seems to have ceased its further growth so that the egg becomes practically seated at the end of the strand running into it. The mycelial strands consist of two systems of tissues: a central or medullary bundle of fine hyphæ running in a longitudinal direction, and an outer or cortical layer of coarser hyphæ forming a loose but very interwoven structure.

The cortical layer of the strand is continued upward in the egg as its outer covering (*C*, *fig. 1*). This figure is from a median longitudinal section of an egg 1.5<sup>mm</sup> long by about 1<sup>mm</sup> in diameter. The more compact medullary bundle is marked *M*. As in the strand, so here, its hyphæ run in a prevailing longitudinal direction lying close together. By the double stain used these two layers of the egg are sharply separated from each other in color as well as by the more open structure of the cortical layer. Although so well marked, still they are in intimate connection in their region of contact by means of hyphæ which spread out laterally from the medullary layer and branch and interlace with the cortical hyphæ and become indistinguishable from them. In *fig. 2* a cross-section of an egg in the same stage

of development as that of *fig. 1* is given under the same magnification. The medullary bundle *M* is nearly circular in cross-section.

A developmental change now sets in through which the outline of the medullary portion becomes lobed. These lobes alternate in position with the later formed columns of the receptaculum and extend longitudinally from near the base of the egg almost to the apex of its medullary bundle. The four such lobes usually formed in *C. columnatus* are shown in the cross-section of an egg in this stage (*G, G, fig. 4*). *Fig. 4* is drawn with the same magnification as *figs. 1* and *2*, the diameter of the egg having become only slightly greater. Many eggs of about the same diameter as these were sectioned and examined in order to find intermediate stages between those of *figs. 1* and *2* and *fig. 4*, which would show the mode of differentiation of the medullary lobes *G, G*. It seems probable that their differentiation occupies only a short interval of time, for only one egg in the intermediate stage was found. It is shown in cross-section in *fig. 3*, and under the same magnification used in the other cases. In this stage (*fig. 3*) the medullary and cortical layers are less sharply distinct from each other than in the earlier or later stages. At three points, perhaps four, hyphæ seem to be invading the cortical region of *fig. 2* and forming masses (*G*). These masses are the rudiments of the gelatinous layer of the volva of later stages. Only three such lobes can be made out with certainty in this stage, while four are present in the more advanced stage of *fig. 4*. The absence of the fourth may indicate that the differentiation of all four lobes does not begin at exactly the same time; but it seems more probable, however, that this is an early stage of a *Clathrus* having three columns for its receptaculum. In such a plant only three gelatinous masses are present in the gelatinous layer of the volva. Specimens having only three columns did occasionally occur in this material.

The rudiments (*G, G, G, fig. 3*) of the gelatinous layer of the volva are most intimately connected with the central medullary mass and must undoubtedly be regarded as belonging to the

medullary system, as they have been heretofore.<sup>3</sup> As shown in this stage the manner of formation of these lobes seems to be that of a general growth of medullary hyphæ along three or four longitudinal lines outward among the cortical hyphæ of the layer *C* of the youngest stage. That this is the actual mode of formation of the lobes is shown by the fact that their marginal portions are less sharply set off from the cortical layer than is the case in later, and even earlier stages. In this stage many cortical hyphæ can be followed into the marginal portions of the lobes, and the color reactions by the double stain used are less sharp in those portions than they are between the cortical and medullary systems in other stages.

It is to be observed that in this stage the surface of the egg does not conform to the surface of the medullary portion, but has in cross-section the nearly circular outline of the youngest stage (*fig. 2*). In later stages a gelatinous accumulation in the lobes (*G, G*) causes them to swell outward and laterally towards each other so as to give to the egg a surface with a broad rounded longitudinal ridge, extending outside of each lobe from the base of the egg nearly to its apex. These lobes are separated by shallow furrows, each of which marks the position of a column of the receptaculum, and is of great help in orienting the eggs for sectioning. Were such longitudinal ridges and furrows present on the surface of the egg in the stage of *fig. 2*, they would have favored the view which I formerly held that the medullary lobes originate by outward protrusion of medullary tissue along four longitudinal lines, such protrusion being due to vigorous growth within the medullary portion merely pushing the cortical layer further outward in those regions.

The columns of the receptaculum arise in the angles (*C', C'*) between the medullary lobes (*G, figs. 3 and 4*). Ed. Fischer<sup>4</sup> in his study of *Clathrus cancellatus* has called the tissue *C'* of these angles *Zwischengeflecht*, and has referred it to the medullary sys-

<sup>3</sup> Cf. Ed. Fischer, Untersuchungen z. vergleich. Entwicklungsgeschichte u. Systematik der Phalloideen. Denkschr. d. Schweiz. naturf. Gesellsch. 32: 4. 1890; also Burt on Anthurus, *l. c.* 494.

<sup>4</sup> *Ibid.* 4.

tem of tissues, although pointing out that its hyphæ are coarser, more highly refractive, more loosely arranged, and more irregularly intertwined than is the case in the rest of the medullary system. In all of these points of difference which have been enumerated, the tissue in question agrees with that forming the surface of the egg. As it is also more intimately connected with such cortical tissue than with the medullary tissue, stains the same as the former, and in the youngest stages (*figs. 1 and 2*) is the direct continuation upward in the egg of the cortical tissue of the mycelial strand, it should be regarded as belonging to the cortical system. It will be referred to in this article as the tissue of the cortical plates, as in my earlier paper on *Anthurus*.

In the earliest stages the cortical layer is closely adnate to the medullary layer. In the stage of *fig. 4* separation of these two layers begins along the inner edge of each cortical plate, the two tissues seeming to be pulled slightly apart, although very numerous hyphal connections still exist between the two surfaces. In the older stage of *fig. 5* this separation has become more complete and a decided fissure has been produced between the two systems along the inner edge of the cortical plate (*C'*). While it is possible that the rapid growth of the medullary lobes (*G*) and their distention with the gelatinous accumulation may have carried the cortical system outward bodily and, to some extent, may have loosened the cortical plates from their connections along their inner edges, it seems more probable that the separation has been caused chiefly by changes in the medullary structure facing against the cortical plates, as shown in *fig. 5*. Medullary hyphæ reaching to the edge of a cortical plate become swollen at the outer end and become arranged side by side in a palisade-layer. Branches of a similar nature crowd their way in between the members of this palisade-layer and so increase its surface that the layer becomes thrown into folds (*t, fig. 5*) and torn away from its connections with the edges of the plates (*C'*). In some of the sections of this stage occasional hyphal connections of this kind still persisted.

Examination of the surface of contact of medullary lobes (*G*) of the volva with the cortical layer (*C*) and the cortical plates (*C'*) shows that the hyphæ in this surface now lie in the plane of the surface, indicating that, in the great increase in the volume of these lobes since the stage of *fig. 4*, their distention (partly due to gelatinous accumulation no doubt) has been pushing their surface bodily against the cortical layer. The same distention of these lobes has also brought them closer together, laterally compressing the masses *C'* of *fig. 4* into the narrower plates of *fig. 5*, and into still narrower plates in the more advanced stage of *fig. 6*.

With the further growth of the egg, the medullary surface (*t*, *fig. 5*) becomes thrown into a very complicated series of folds, causing passages to extend in a labyrinthine manner into the main central medullary mass. The cells of the palisade-layer facing the deeper lying passages differentiate into basidia and bear spores. This portion constitutes the gleba (*Gl*) of older stages. Hyphæ from the cortical plates penetrate into the passages situated in front of the edges of the cortical plates, become adnate to the surfaces of the medullary masses (*t*) forming the walls of those passages, differentiate into pseudoparenchyma, and prevent the differentiation of basidia and spores on the surfaces covered. The pseudoparenchyma so formed constitutes the walls of the receptaculum of later stages; the medullary tissue (*t*) enclosed by these walls is the tissue of the chambers of the receptaculum, and it gelatinizes and becomes torn up in the elongation of the receptaculum, leaving the chambers empty for the most part. The relation of these tissues to each other are represented in *fig. 6*. At the right the medullary tissue (*t*) is shown with its hymenial layer of basidia lining the cavities or passages of the gleba. Just to the right of the cortical plate (*C'*) a column of the receptaculum is developing; cortical hyphæ from *C'* have grown into the passages between the medullary masses (*t*) and, in contact with those masses, are developing into pseudoparenchyma. The depth to which the cortical hyphæ have invaded these passages is shown

by the position of the continuous line *q* in the figure. Beyond that line basidia line the passages. At *r*, *r*, *r*, medullary masses may be seen crossed by the line; these masses lie partially in the gleba and partially in the column. In their glebal portion they bear a layer of basidia; on the ends in the column they are covered with the cortical tissue. It is by such connecting medullary masses that the gleba hangs suspended within the cavity of the receptaculum after elongation of the latter.

In the same figure (*fig. 6*) many medullary masses (*t*) may be seen in the column not connected with the other masses to the right. These unconnected masses are in general smaller toward the edge of the cortical plate (*C'*) and, in some stages, they are more closely surrounded by the adhering cortical tissue than are the masses at a greater distance from the edge of the plate. Ed. Fischer has described the occurrence of such isolated masses,<sup>5</sup> which he calls hyphal knots (*Hyphenknäuel*) in *Clathrus cancellatus*, and has concluded that they arise from the differentiation of the tissue of the cortical plates.<sup>6</sup> In this opinion I cannot concur. As already stated, my preparations show that a continuous cavity is first formed between the edges of the cortical plates and the medullary tissue. Hyphæ from the one side of this cavity grow into it. Along the opposite side of the cavity branching masses of medullary tissue extend into the cavity, partially filling it and causing its irregularity in form. Such medullary masses are represented by the dark areas in *figs. 10-13*. They are highly gelatinous, having the same microscopic structure as that of the gelatinous layer of the volva and the main central mass of medullary tissue, and they take the same orange-red stain in my preparations. *Figs. 10-13*, in the order of their numbering, represent serial cross-sections, of which *fig. 10* is of the section at the lower end of the series, or nearest the base of the egg. They are from below the level of the gleba. The examination of such a series of cross-sections affords reason

<sup>5</sup> *Ibid.* 5, *figs. 3 and 4*.

<sup>6</sup> Fischer calls this tissue *Zwischengeflecht*. It is, however, a wholly different tissue from that to which he applies the same name in the *Phallæ*.

for believing that these gelatinous masses are all connected with each other and with the main central mass of medullary tissue. In *fig. 10* an irregular mass occurs consisting of five main parts, each of which is marked 1. Upon following this mass upward through the series, it is found that its five parts finally become separate from each other, and that the outermost part of the original mass does not reach up into the plane of the highest section (*fig. 13*). The small mass marked 2 also fails to reach up into that section. The attempt to follow in serial sections the apparently isolated masses (Fischer's "hyphal knots") of any one section leads to the conclusion that such masses are portions of a highly branched structure arising from the inner main medullary mass, and that the ramification of this mass is outward and chiefly upward. Such a branched structure along the medullary side of the cavity has arisen, without doubt, partly from the folds produced by the formation of the palisade-layer, as already described; but there is evidence that it may be due in part also to an irregular splitting downward and inward into the medullary tissue, as shown by the changes that occur in the connections of the cavity 3 (*figs. 10-13*), and by the fact that masses, joined together into one in some sections, become separate in others, and then join again into one. Other evidence is afforded by the distribution among the medullary masses of hyphæ from the cortical plates. In this stage such cortical tissue is found in greatest abundance in the marginal portions of the cavity; it is almost wholly absent from some, but not all, of the spaces between the more centrally situated masses.

The medullary masses which we have been considering occupy spaces which become the chamber-cavities of the receptaculum in later stages. Although portions of *t*, they are more definitely indicated by *b* in *figs. 6-9*, and *14*.

*Walls of the receptaculum.*—The tissue of a cortical plate (*C'*) forms a broad layer of loosely interwoven and branching hyphæ, divided into short cells. This tissue is quite similar to that of the cortical layer (*C*) with which it has unbroken connection. Along the inner edges of the cortical plates, their tissue passes

into the cavity which has formed there, and spreads about in it, and between the medullary masses (*b*), and over the surfaces of those masses and on that of the cavity. For some reason (which may, perhaps, be proximity to a supply of available food) these cortical hyphæ find the conditions for their further differentiation most favorable on the surfaces of the masses of gelatinous tissue, and they become closely adherent to such surfaces and grow very luxuriantly there. Still, many of the hyphæ are found in the more open space, running irregularly through such spaces or crossing from one side to the other. It is this tissue which finally fills the spaces between and about the gelatinous masses and becomes the chamber walls of the receptaculum.

An older stage of the rudiment of a column of the receptaculum and of the tissues about it is shown in cross section in *fig. 7*. \* On the right is the tissue of the gleba with its chambers lined by the hymenial layer (*H*). On the left is the inner edge of a cortical plate (*C'*); its hyphæ may be seen passing among and against the medullary masses (*b*) of the future chambers. These cortical hyphæ are becoming laterally inflated in this region and are plainly recognizable as early stages of pseudoparenchyma. Along the surfaces of the larger cavities, the development of these hyphæ is giving rise to pseudoparenchymatous plates (*p, p*) which in later development have the intervening space more filled in with this tissue, forming a more compact partition wall. Near the gleba, large masses (*b*) of the tissue of the chambers are connected, as in *fig. 6*, with the tramal tissue (*t*) and with the tissue on the inner flanks of the column of the receptaculum, tissue just on the border between the gleba and the gelatinous layer of the volva. At places in the cross-section where the two systems of tissues come into most intimate contact and where the plane of the section may happen to give a cross-section of the pseudoparenchymatous hyphæ, it becomes very difficult to determine the true relations to each other of the adnate tissues *p* and *b*. I have examined such places with the utmost care and find no connections between the tissues of the chambers and the pseudoparenchyma of the walls. If such

connections exist in *C. columnatus*, they should show as distinctly as they do in *Mutinus caninus* or in *Dictyophora duplicata*.

At other places in the preparation the pseudoparenchymatous hyphæ may happen to lie in the plane of the section. In such places, in preparations double-stained with paracarmin and safranin, the true relations of the pseudoparenchyma and the tissue of the chambers become clearly shown, as in *fig. 8*. In this figure the wall (*p*) is shown with the tissue of a chamber (*b*) on one side and with the gelatinous layer of the volva (*G*) on the other. The pseudoparenchyma of the wall has no connection with either the tissue of the chamber or with that of the gelatinous layer of the volva. It has merely taken possession of a space between the two. If this figure is compared with *figs. 11, 12 and 15* of my paper on *M. caninus*, the contrast between the Clathræ and the Phallæ in the origin of the pseudoparenchyma becomes very evident. There is also a difference in appearance between the gelatinous tissue in the chambers of *C. columnatus* and that in the chambers of the Phallæ which I have seen. In the former there is a very marked resemblance to the tissue of the gelatinous layer of the volva. This may be seen also in *fig. 8*.

Ed. Fischer<sup>7</sup> has asserted that the pseudoparenchyma of the walls of Clathrus is homologous with the hymenial layer, being merely a sterile hymenium. The portion of the section drawn in *fig. 9* is of great importance in this connection. It represents a portion of a column and the adjacent gleba. In the upper part of the figure, the basidia of the hymenium (*H*) are seen projecting radially outward from the tramal tissue (*t*) into a chamber of the gleba. The wall (*p*), consisting of pseudoparenchymatous hyphæ, is situated between the tramal tissue and the gelatinous tissue (*b*) of a chamber. The hyphæ of the wall are slightly laterally inflated. They are not connected with the tissue of the chamber or with the gleba. If the homology put forth by Fischer were well-founded, the pseudoparenchyma should have the same connection with the tissue of the chamber

<sup>7</sup> *Ibid.* 7.

that the basidia have with the tramal tissue, and should also project from the chamber surface perpendicularly outward into the cavity between the chamber masses.

*Advanced stages.*—A median longitudinal section through an old egg is given in *fig. 14*. The section is also median with respect to the columns of the receptaculum, one of which is shown on the right. The beginning of elongation of the receptaculum has torn the glebal mass away from the lower part of the medullary mass. Near the upper end of the column, along its inner side, many more openings show in the wall than further down toward the base. Through these openings the medullary tissue passes into the chambers and firmly attaches the gleba to this portion of the receptaculum. The figure shows how in the mature stage the ball of glebal tissue comes to be suspended from the under side of the apex of the receptaculum.

A more important point presented by *fig. 14* is the manner in which the cortical and medullary systems of tissues are dovetailed together in the receptaculum. From the left an originally continuous mass of medullary tissue sends branches towards the right; from the right an almost continuous mass of pseudo-parenchyma sends branches towards the left, filling in all space between the first set of branches.

This section does not show many of the openings in the wall near the base of the receptaculum, through which the medullary hyphæ pass into the lower chambers. Openings of that nature do, however, exist, although they are not so numerous there as higher up. One such passage into a chamber is shown on the left side of the figure.

#### REFERENCE TO ANTHURUS BOREALIS BURT.

In my account of the structure and development of *Anthurus borealis*, one of the Clathreæ, it was shown that cortical plates extend from the base of the egg upward almost to the apex, and inward from the cortical layer to the receptaculum. In the region below the level of the base of the arms, the inner edges of the plates are united into one cylindrical mass which forms a

sheath of cortical tissue (the cortical sheath) surrounding the stipe for its whole length.

The pseudoparenchyma of the walls of the stipe and of the arms was found connected with and arising from the tissue of the cortical sheath and cortical plates. Medullary tissue from the main central mass was found passing into the chambers of the receptaculum at the base of the stipe and then passing upward from chamber to chamber. At the base of the arms, the ascending masses of medullary tissue are collected into six large masses, each of which is the gelatinous tissue of an arm. No connection could be found between the pseudoparenchyma and the gelatinous tissue of the chambers nor did the pseudoparenchyma stand out from the sides of the chambers so as to indicate any such connection.

The conclusion was reached that in *A. borealis* the receptaculum is formed by the joint action of both cortical and medullary tissues; that the cortical constituent develops into the pseudoparenchyma of the walls, and that the enclosed medullary bundles finally become gelatinous and disappear, thus forming the chambers of the wall.

#### CONSIDERATION OF FISCHER'S VIEW OF THE ORIGIN OF THE RECEPTACULUM IN THE CLATHREÆ.

Ed. Fischer<sup>8</sup> has stated in his study of the development of *Clathrus cancellatus*, to which references have been made:

1. That the fundament of the receptaculum consists of knots of hyphæ separated from one another by small spaces.

2. That these hyphal knots are formed from the *Zwischengeflecht* (in this case the tissue of the cortical plates *C'* of my figures).

3. That the tips of the hyphæ composing the knots radiate outward from the knots into the narrow spaces between the knots and become constricted and abjoined into pseudoparenchyma, thus forming a plate about each knot.

4. That the tissue in the central portions of the knots

<sup>8</sup> *Ibid.* 5-8.

becomes gelatinous and finally disappears, giving rise to the chamber cavities.

5. That since the tissue of the knots is found to be in connection with the tramal tissue of the gleba at some points, therefore it follows that the receptaculum and the gleba are homologous, that the tissue of the chambers of the former is identical with the tramal tissue of the latter, and that the pseudoparenchymatous walls of the receptaculum chambers are homologous with the hymenial layer of the gleba.

Comparison of Fischer's *figs. 5* and *7* with my *figs. 6* and *7* shows that we both see the same general structure and that our difference is in its interpretation. That Fischer's interpretation of the structure is not the correct one seems to me to be shown by the following considerations:

1. The existence in the Clathreæ of the supposed hyphal knots is very doubtful. My experience is that if the attention is fixed upon one of them, and this is then followed through section after section of the series, the supposed "knot" is soon found to be connected with other masses, and so on with the main medullary mass.

2. The tissue of the cortical plates *C'* (*Zwischengeflecht* of Fischer) does not form hyphal knots. About small medullary branches located in the densest portion of the tissue *C'*, as at *2*, *fig. 9*, it often happens that the plane of the section will be unfavorable for displaying the true relations of the two closely adnate tissues. At such a place one needs all of the aid to be had from good double-stained preparations.

3. If pseudoparenchyma of the chamber walls arises from the hyphæ of the chambers by the projection of the swollen hyphal tips outward into the narrow intervening spaces, it ought to be found distinctly connected with the tissue of the chambers, as in the Phalleæ, and its short hyphæ should also be found projecting from the sides of the chamber masses into the narrow spaces in directions perpendicular to the surfaces of the chambers. Such a direction of the pseudoparenchymatous hyphæ should be shown distinctly, as it is in the Phalleæ. In

some parts of the section, where the pseudoparenchymatous hyphæ are closely crowded against the chamber tissue, and where the plane of the section has cut these hyphæ transversely, one must be on his guard against mistaking the cut ends of adjacent pseudoparenchymatous hyphæ for pseudoparenchymatous bodies standing out perpendicularly from the sides of the chambers. Such closely crowded cut ends, with their looser arrangement toward the middle of the space, form a block-like structure very well adapted for giving the familiar optical illusion of radiation.

I fail to find hyphal connection between the pseudoparenchyma and the tissue of the chambers, nor is there an arrangement of the pseudoparenchymatous hyphæ perpendicular to the surface of the chambers. On the contrary, wherever the plane of the section discloses the arrangement, these hyphæ are found lying parallel with the surfaces of the chamber masses, as shown in *figs. 8 and 9*. If Fischer's theory were true, such an arrangement should not be found at any point.

4. Since the homology claimed between the pseudoparenchyma and the hymenial layer of *Clathrus* depends upon the origin of pseudoparenchyma from the tissue of the chambers, it ceases to be tenable.

The theory of the origin of the receptaculum enunciated by Ed. Fischer has been accepted by A. Möller<sup>9</sup> in his interesting and instructive work on the Brazilian Phalloideæ. His investigation seems to have been completed and his work in process of publication when my paper on *Anthurus* reached him, as his references to it are in footnotes.

#### SUMMARY FOR THE CLATHREÆ.

In the earliest stage, the egg consists of cortical and medullary systems continued upward from the mycelial strand.

The cortical layer gives rise to the outer layer of the volva, the cortical plates, and the pseudoparenchyma of the receptaculum. The medullary portion gives rise to the gelatinous masses

<sup>9</sup> Brasilische Pilzblumen. Jena, 1895.

of the gelatinous layer of the volva, to the gleba, and to the gelatinous tissue of the chambers of the receptaculum.

In such differentiation, the gelatinous masses of the volva are the first to be set off. They arise by growth outward into the cortical region of the hyphæ from several areas of the medullary mass.

The masses of cortical tissue which separate the medullary gelatinous outgrowths from each other retain their connection with the outermost layer through all the later development of the egg. They may be called cortical plates; their position is indicated by shallow furrows on the surface of the egg.

Along the inner edge of each cortical plate, a cavity forms by the separation of the two systems of tissue in that region. The medullary tissue facing these cavities gives rise to the gleba and to branching hyphal masses, which project outward and upward into the cavities and become the chamber tissue of the receptaculum.

The receptaculum is formed through the joint participation of the two systems of tissue and differs in its origin and mode of formation from that of the Phalleæ. Its chambers have the position originally occupied by a branched structure of medullary origin, while its pseudoparenchymatous walls form by ingrowth of cortical tissue about and between the chamber masses.

The pseudoparenchyma of the walls is not homologous with the hymenial layer.

The elongation of the receptaculum in *C. columnatus* begins at the base. After elongation of the receptaculum, the gleba hangs suspended from the arch of the receptaculum by medullary tissue constituting chamber masses of the receptaculum.

#### RELATIONSHIP OF PHALLEÆ AND CLATHREÆ.

The Phalleæ and the Clathreæ, the two usually accepted sub-orders of the Phalloideæ, resemble each other:

1. In gross structure. Both have a volva of the same general structure, which becomes ruptured by the same means and from which there issues the receptaculum.

2. In microscopic structure. Both have a gleba of the same chambered structure, with basidia lining the chambers and bearing numerous (4-8) very minute spores. Both have a receptaculum of chambered structure, with walls of irregularly laterally inflated hyphæ, the pseudoparenchyma.

3. In biological adaptation for combining a safe early development with a good means of dissemination of the mature spores. In both the early development is subterranean, in the form of a compact egg covered by a thick gelatinous coat retentive of moisture and probably protective. When the spores are mature they are quickly raised above ground, and an attractive lure for insect agency in their dissemination is then offered by the fetid odor and saccharine composition of the deliquescent mass in which they lie, as well as by the bright colors of the receptaculum which supports them.<sup>10</sup>

The differences between these two subfamilies are no less significant. They are shown:

1. In the mature stage. The position of the gleba is outside the receptaculum in the Phalleæ, while it is within that structure in the Clathreæ. The gelatinous layer of the volva is a continuous sheet in the Phalleæ, while in the Clathreæ it is separated by the cortical plates into several more or less connected masses, wholly separate from each other in *Clathrus*, but joining above into one in *Anthurus*.

2. In early development. (a) In early differentiation of the Phalleæ, the steps by which the lower and lateral portions of the sheaf-like head (those portions bearing the future hymenium) lose their original direct connection with the medullary bundle *M* and become split away, as it were, from the stipe from below, have no parallel in the Clathreæ, and remind one rather of the changes that occur in the formation of the pileus in some *Agaricineæ*. (b) The hymenium of the Phalleæ arises underneath the gelatinous layers of the volva on the inner (under)

<sup>10</sup> (a) W. R. Gerard, Bull. Torr. Bot. Club 7: 30. 1880; (b) Rathay und Haas, Ueber *Phallus impudicus*, (L.) und einige Coprinus-arten, Sitzungsab. d. Mathem.-Naturwiss. Akad. zu Wien 87: 18. 1883; (c) Fulton, Dispersion of spores of fungi by insects, Annals of Botany 3: 207. 1889.

side of the peripheral portions of the sheaflike head, while in the Clathreæ its portions alternate with the gelatinous lobes of the volva. (c) The basidia of the young hymenium of the Phalleæ face towards the axis of the plant; in the Clathreæ they face in the opposite direction, towards the periphery. (d) In the Phalleæ, tissue of medullary origin gives rise both to the pseudoparenchyma of the receptaculum and to the tissue of its chambers; in the Clathreæ, cortical tissue continuous with that of the mycelial strand forms the pseudoparenchyma,<sup>11</sup> while the tissue of the chambers is of medullary origin and connection.

The marked resemblances that have been pointed out between the mature stages of the Clathreæ and Phalleæ have been regarded in systematic botany as sufficient for joining them into a well-marked order, the Phalloideæ. The difference in the position of the gleba, whether on the outside of the receptaculum or within it, has been made the basis of their separation as suborders.

Rehsteiner's work<sup>12</sup> on *Hysterangium clathroides* and *Hymenogaster decorus*, both belonging to the Hymenogastreæ, led him, on the ground of the position of the hymenium and the direction in which it faces, to point out a probable origin of the Clathreæ from a *Hysterangium*-like ancestor, and a possible origin of the Phalleæ from one of the Hymenogastreæ near *Hymenogaster*, a view Ed. Fischer has also since expressed.<sup>13</sup>

Thaxter's account of *Phallogaster saccatus*<sup>14</sup> indicates that this may be a species somewhat closer to the Clathreæ than *Hysterangium clathroides* is, on account of having a gelatinous layer

<sup>11</sup> That the pseudoparenchyma of the receptaculum of the Clathreæ is cortical in origin is not strange. A. Möller states that in *Clathrus columnatus* and *Blumenavia rhacodes* the cortical layer of the mycelial strands is pseudoparenchymatous (Brasilische Pilzblumen 143), and that in the latter species it is so highly pseudoparenchymatous as almost to lose its hyphal characters (*ibid.*, 61). Both of these species are Clathreæ.

<sup>12</sup> Rehsteiner, Beiträge z. Entwicklungsgeschichte d. Fruchtkörper einiger Gastromyceten. Botanische Zeitung. 50; — (38-40). 1892.

<sup>13</sup> Neue Untersuchungen d. Phalloideen. Denkschr. d. schweiz. naturf. Gesellsch. 33<sup>1</sup>: 44. 1893.

<sup>14</sup> Note on *Phallogaster saccatus*. BOT. GAZ. 18: 117. pl. 9. 1893.

between its gleba and peridium that is to be regarded, probably, as the forerunner of the gelatinous masses in the volva of the Clathreæ.

A. Möller's description of his *Protrubera Maracuja* makes a still closer connection.<sup>15</sup> He finds not only gelatinous masses next to the peridium, but also finds them arranged alternately with reference to the glebal masses, as in the Clathreæ, and separated from each other by cortical plates along whose inner edges the glebal masses develop. The development of the cortical plates from the peridium, and their connection with it, are made very probable by his *figs. 2-5, pl. VI.*

My studies, showing that the pseudoparenchyma of the receptaculum of the Clathreæ is of cortical (peridial) origin, supply another link in the chain connecting the Clathreæ with Hysterangium. By making known the early differentiation of the Phalleæ, and by showing that this subfamily differs wholly from the Clathreæ in the development of the receptaculum, they make it certain that the Phalleæ, although as highly a differentiated subfamily, cannot have arisen from the Clathreæ.

It seems safe to conclude:

1. That the Phalleæ are not directly related to the Clathreæ.
2. That both subfamilies have arisen from lower forms outside their family.
3. That the Phalloideæ consist of two parallel series of forms, which, through variations from unlike starting points, have attained to highly specialized structures adapted to the same ends.

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#### EXPLANATION OF PLATES XI AND XII.

All figures were drawn with the aid of an Abbé camera lucida. The following letters are common to all the figures: *C*, cortical layer; *C'*, cortical plate; *G*, gelatinous layer of volva; *GL*, gleba; *H*, hymenium; *M*, medullary bundle of young stages; *b*, tissue of the chambers; *i*, inner layer of the volva; *p*, pseudoparenchymatous wall of the chambers; *t*, tramal tissue.

<sup>15</sup> *Ibid.* 10.

FIG. 1. Median longitudinal section of the youngest egg.  $\times 60$ .

FIG. 2. Cross-section of an egg in the same stage of development as that of *fig. 1*.  $\times 60$ .

FIG. 3. Cross-section of a slightly older egg, in which differentiation of the gelatinous masses of the volva has just begun. It is doubtful whether this would give rise to three such masses or to four, in the former case with a receptaculum having three columns alternating with the masses, or in the latter to one with four.  $\times 60$ .

FIG. 4. Cross-section of an egg in a still older stage, with four masses (*G*) forming the gelatinous layer of the volva. The four columns of the receptaculum arise in the angles between these masses along the inner edges of the cortical plate (*C'*).  $\times 60$ .

FIG. 5. Portion of a still older egg in cross-section, showing an early stage in the formation of a cavity between the cortical plate (*C'*) and the deep-lying medullary portion (*t*). One column of the receptaculum arises in a part of each such cavity; the hymenium arises along the surfaces of the remaining part.  $\times 60$ .

FIG. 6. The same region of the egg shown in *fig. 5*, but in a more advanced stage. The column is now developing. The sharp continuous line, *q*, has been drawn to more clearly set off the column from the gleba. At the places marked *r, r, r*, medullary masses connect the tissue of the chambers of the receptaculum with the tramal tissue of the gleba.  $\times 34$ .

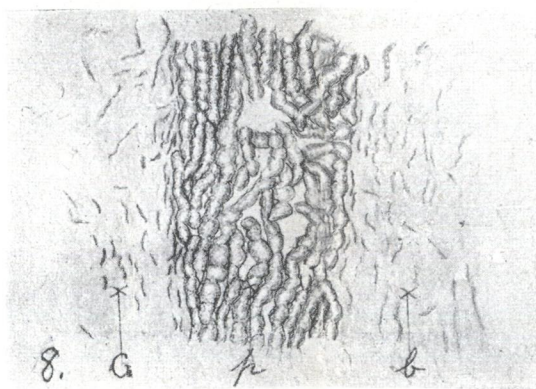
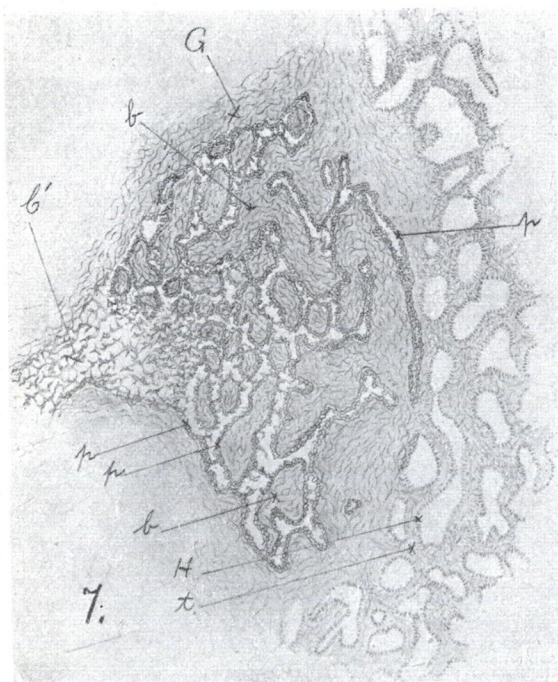
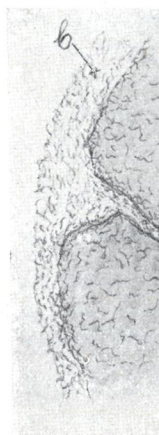
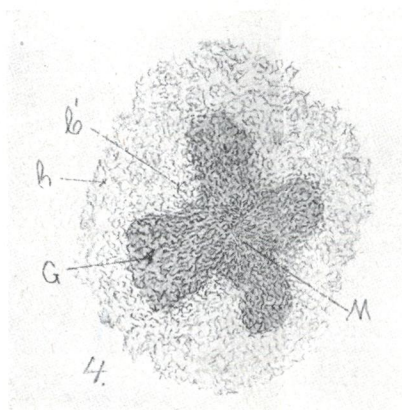
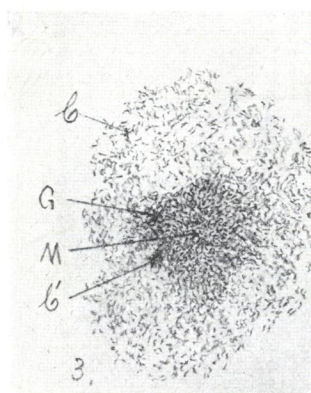
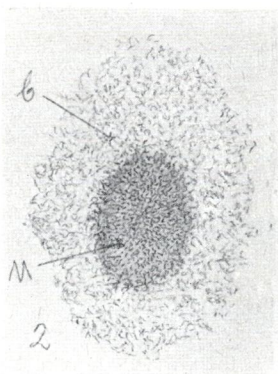
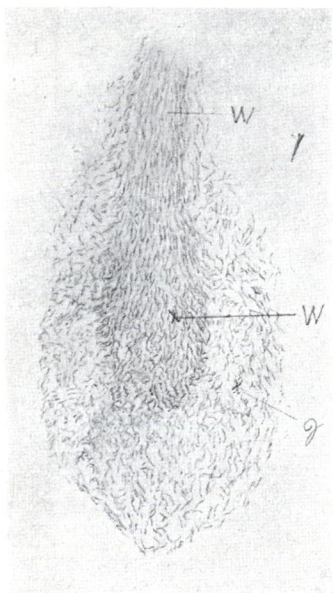
FIG. 7. Cross-section of a fundament of a column of the receptaculum, showing medullary connections of the chamber tissue towards the right and cortical connections of the pseudoparenchyma towards the left.  $\times 34$ .

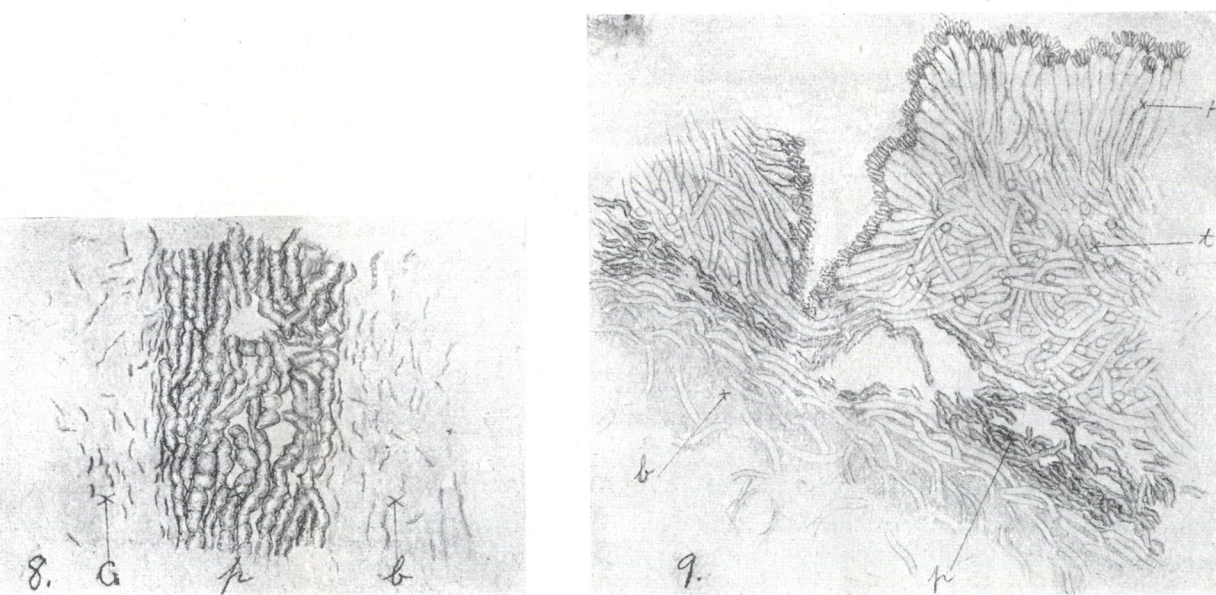
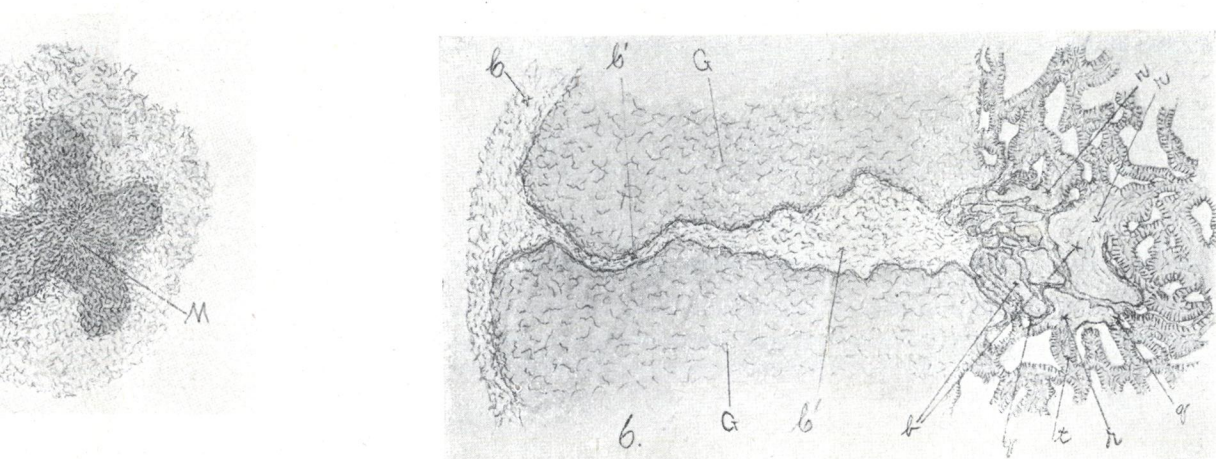
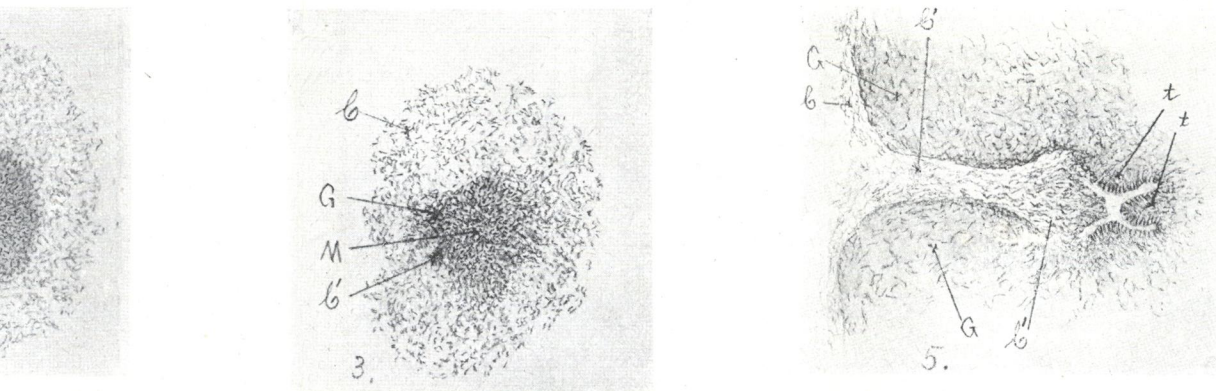
FIG. 8. Portion of the wall, *p*, of *fig. 7*, more highly magnified.  $\times 670$ .

FIG. 9. Portion of the wall, *p*, between the gleba (*Gt*) and a chamber mass (*b*) of *fig. 7*.  $\times 325$ .

FIGS. 10-13. Serial sections of chamber-masses of a column, with adjacent tissues, in the lower part of the egg. *Fig. 10* represents the lowest section. The series shows how the small and apparently isolated masses ("hyphal knots") are in reality connected with the main medullary mass.  $\times 106$ .

FIG. 14. Median longitudinal section through an egg in which elongation of the receptaculum is beginning. Shows a column in longitudinal section displaying its relations to other structures.  $\times 6$ .







BURT on CLATHRUS.